

Recovery Potential of Dune Ecosystems Invaded by an Exotic *Acacia* Species (*Acacia longifolia*)¹

HÉLIA S. MARCHANTE, ELIZABETE M. MARCHANTE, ERIKA BUSCARDO, JOSÉ MAIA, and HELENA FREITAS²

Abstract: The effect of mechanical clearing and litter removal on control of Sydney golden wattle was studied in areas of Portugal that had been invaded for either long or short periods. The plant species that emerged and soil parameters were monitored to assess the recovery potential and the soil status of these areas after Sydney golden wattle control. More plant species emerged in the plots where mechanical control in combination with litter removal was applied than in nontreated plots or in plots where mechanical control alone was used. More plant species emerged in the recently invaded areas than in those that had been invaded for a long time. More Sydney golden wattle seedlings were found in the long-invaded area than in the recently invaded one. Total litter, nitrogen and carbon content, and β -glucosaminidase activity were higher in the soil of the long-invaded compared with the recently invaded areas. Regarding the efficacy of the methods used to remove Sydney golden wattle, sprouting was not observed 10 mo after cutting the trees in both areas, although this was not the case in other parallel studies.

Nomenclature: Sydney golden wattle, *Acacia longifolia* (Andrews) Willd.

Additional index words: Invasive plants, mechanical control, native species recovery, soil properties.

Abbreviations: A, with *Acacia longifolia*; AR, *Acacia longifolia* removed; ALR, *Acacia longifolia* and litter removed; NAG, *N*-acetyl- β -D-glucosaminidase (NAGase EC 3.2.1.30); NRSJD, Natural Reserve of São Jacinto Dunes.

INTRODUCTION

Many natural and seminatural areas are being invaded by exotic plant species, leading to the degradation of many ecosystems in the world (Mooney and Hobbs 2000). Mediterranean ecosystems are among the most seriously affected, with alarming decreases in biodiversity and changes to ecosystem processes, particularly fire regimes and the erosion processes (van Wilgen et al. 1996).

One of the most threatening invasive plant species in the Portuguese dune ecosystems is Sydney golden wattle. This species was planted at the beginning of the last century to curb sand erosion but has now proliferated and is causing significant negative ecological impacts

(Alves et al. 1998; Marchante 2001; Marchante et al. 2003). The genus *Acacia* includes about 1,200 species, the majority being native to Australia and Southern Africa (Whibley 1980). It belongs to the subfamily *Mimosoideae*, of the family *Fabaceae*, which includes several of the worst invasive plant species in the world (Cronk and Fuller 1995). The successful establishment of the *Acacia* species could be attributed to its prolific seed production, with extensive longevity in the soil, high viability, and stimulation of germination by fire (Crawley 1997) as well as rapid growth of the plants and high survival in the absence of natural enemies (Callaway and Aschehoug 2000). Their ability to fix nitrogen (*Fabaceae*) has enabled them to invade nutrient-poor environments (Milton 1981). The genus *Acacia* is absent from the Portuguese native flora, but more than 12 species were introduced (Paiva 1999), several of which have become a serious threat to native ecosystems (Marchante et al. 2003; Tavares et al. 1999).

A decline in species diversity attributable to invasive plant species (Binggeli 1996; Lodge 1993) has been

¹ Received for publication January 30, 2004, and in revised form May 3, 2004.

² First and fourth authors: Adjunct Professor and Researcher, Departamento de Ciências Exactas e do Ambiente, Escola Superior Agrária de Coimbra, Bencanta, 3040-316 Coimbra, Portugal; second, third, and fifth authors: Ph.D. Student, Technical fellowship, and Full Professor, Departamento de Botânica, Universidade de Coimbra, Calçada Martim de Freitas, 3000 Coimbra, Portugal. Corresponding author's E-mail: hmarchante@mail.esac.pt.

demonstrated for some *Acacia* species (Holmes and Cowling 1997; Marchante et al. 2003), possibly leading to profound changes in functioning and structure of ecosystems (Lonsdale 1999). Soil physical and chemical properties (Musil 1993) and microbial activity can be altered by the presence of exotic species (Ehrenfeld et al. 2001; Kourtev et al. 2002). N-fixing trees, such as *Acacia* species, can promote enrichment of soil, particularly in ecosystems where soils are naturally poor (Milton 1981; Musil 1993).

This work aimed to study the effect of mechanical clearing and litter removal on control of Sydney golden wattle in two invaded areas of Portugal and to evaluate the recovery of native species after these treatments.

MATERIALS AND METHODS

Study Area. The experimental area, Natural Reserve of São Jacinto Dunes (NRSJD), located in central-northern coast of Portugal, was selected for this study because of its high conservation value. In this ecosystem, the invasion by Sydney golden wattle represents a serious ecological problem, threatening its conservation. NRSJD has about 660 ha and is surrounded by the Atlantic Ocean to the west and by a delta or estuary—Ria de Aveiro—to the east. The area is subject to some degree of human pressure mainly because of tourism and seasonal activities. Despite its conservation status, a large area of the reserve is presently invaded by Sydney golden wattle and, to a minor extent, iceplant [*Carpobrotus edulis* (L.) N.E.Br.] and pampas grass [*Cortaderia seloana* (Schultes) Asch. & Graebner].

Experimental plots were located at least 100 m behind the primary dune system, where sediments have already stabilized and sand mobility is very low. After the invasion by Sydney golden wattle, the open vegetation characterized by small trees, shrubs, and herbs was replaced by almost monospecific, arboreal stands of Sydney golden wattle, causing a significant change in the community structure (Marchante 2001; Marchante et al. 1999).

Experimental Design. Two experiments were carried out in two areas that were invaded at different times by Sydney golden wattle. The first experiment was established in an area where Sydney golden wattle had been deliberately planted at the beginning of the 20th century, whereas the second one was in an area that had only been invaded since 1995 after severe brush fires. In both experiments, a completely random design was used. Fifteen 10- by 10-m plots were demarcated in each region.

Five of the plots were cleared of Sydney golden wattle by cutting the trees with chainsaws at ground level (AR). Another five plots were treated in the same way, but the leaf litter was also removed as an additional treatment (ALR). The remaining five plots served as untreated controls (A). In each plot, 10 subplots of 2 by 2 m were demarcated to record the plant species that emerged after treatments. To reduce variability, the means of five subplots were used for the ANOVA, and mean differences were separated with LSD test at 5% level of significance. The Sydney golden wattle seedlings were counted within the plots during early December and again in February, May, and July.

To measure soil parameters, three soil samples (0- to 10-cm depth) were taken from each plot and analyzed for total nitrogen (Kjeldahl method, Bremner 1965), carbon (Tinsley method, Silva 1977) nitrate and ammonium (extracted with 1 M KCl and analyzed with autoanalyzer), phosphorus (Watanabe and Olsen 1965), and pH (Mc Lean 1982). In all plots except the ones where litter was also removed, samples were also analyzed for *N*-acetyl- β -D-glucosaminidase (NAG) activity (adapted from Miller et al. 1998). Before treatments were applied to the plots, samples of litter were collected, oven-dried, quantified, and analyzed for total nitrogen (as above) and carbon (Baize 2000). The results from plots where Sydney golden wattle was removed (AR) and from plots where Sydney golden wattle and litter were removed (ALR) were compared with those from the unchanged plots where Sydney golden wattle remained (A). To reduce variability, the mean of the three samples were used for the ANOVA. A separate ANOVA was performed for each experiment, and mean differences were separated with LSD test at 5% level of significance.

RESULTS AND DISCUSSION

Sydney Golden Wattle Recovery. The mechanical control operation seems to have been highly successful because 10 mo after the stumps were cut, not a single sprout was observed. Although mechanical control has been demonstrated to be efficacious (Weber 2003), the plants do not always succumb, and about 40% stumps have been seen to resprout approximately 1 mo after the cutting operation during equivalent experiments (H. S. Marchante and E. M. Marchante, personal observation).

The counts of seedlings emergence were extremely heterogeneous between replicates, making statistical analysis impossible. Nevertheless, the total number of seedlings germinating in long-invaded plots once the old trees were removed (Figure 1) was apparently higher,

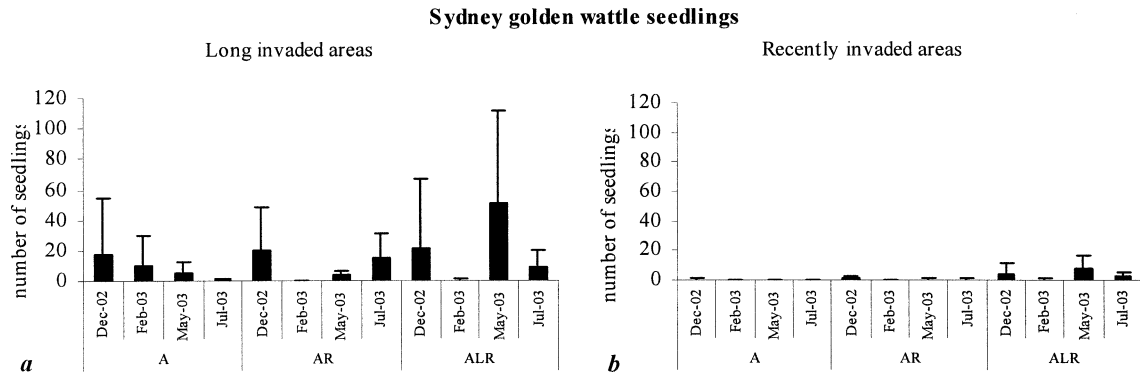


Figure 1. Sydney golden wattle seedlings 3, 5, 8, and 10 mo after the start of the experiments. A, with Sydney golden wattle; AR, Sydney golden wattle removed; ALR, Sydney golden wattle and litter both removed. Bars are average number + SD ($n = 10$).

suggesting that as the invasion proceeds, the invasive potential is enhanced as a result of the increase of seeds of the invasive species. Despite the high number of seeds that germinated (Figure 1), a significant number did not survive; in long-invaded areas where only Sydney golden wattle was removed, more seedling survival was apparent, suggesting that the species' own litter is facilitating its survival. The abundant seedling germination, and their subsequent dead, highlights the importance of maintenance control procedures, including pulling off the seedlings—after about 1 yr, when only the surviving plants are present.

Species Recovery. Ten months after the treatments, both long-invaded (Figure 2a) and recently invaded (Figure 2b) areas showed more species on plots where both Sydney golden wattle and litter (ALR) were removed. This trend indicates that litter removal allows more species to germinate in the short term and thus enhances the rate of recovery of the system. Other authors (Holmes and Cowling 1997) have already mentioned the importance of the removal of the *Acacia* litter to the recovery of previously invaded areas. In control areas where Sydney

golden wattle remained (A) both ages of invasion showed a very low numbers of native species. The shading effects of the closed canopy, altered soil characteristics, and high litter levels alone or in combination may account for the exclusion of native species. Notably, in the long-invaded areas where the litter was left (AR), low numbers of native species germinated, being statistically equal to the control areas ($P = 0.98$). Two possible factors may have a cumulative effect on these differences: (1) after protracted invasion viable seed banks of other species become depleted, and (2) the litter layer is much thicker in long-invaded areas (see text below) and suppresses germination or acts as an impenetrable barrier to the entrance of new propagules. As with previous studies on *A. saligna* (Holmes and Cowling 1997; Musil 1993), recently invaded plots had more plant species germinating than long-invaded plots.

Species germinating belonged mainly to *Asteraceae* (*Compositae*) (30%), *Poaceae* (*Gramineae*) (14%), and *Caryophyllaceae* (12%) (Table 1) The last family was almost exclusive to recently invaded areas. Milton (1981) reported the prevalence of grasses on areas re-

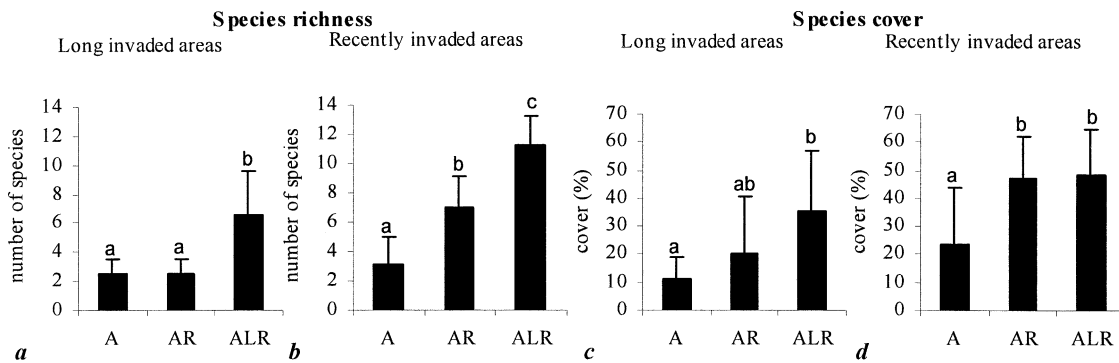


Figure 2. Species richness (a, b) and species cover (c, d), 10 mo after the start of the experiments. A, with Sydney golden wattle; AR, Sydney golden wattle removed; ALR, Sydney golden wattle and litter both removed. Bars are average number + SD ($n = 10$). Different letters in bars of same graphic indicate differences statistically significant at $P < 0.05$ (LSD test).

Table 1. Species (and respective family) colonizing the study plots, and the number of plots of each treatment where each species was registered (A, with Sydney golden wattle; AR, Sydney golden wattle removed; ALR, Sydney golden wattle and litter both removed).^a

Species	Family	Long-invaded areas			Recently invaded areas			Species condition
		A	AR	ALR	A	AR	ALR	
<i>Sagina maritima</i> G.Don	Caryophyllaceae	—	—	—	—	3	12	Dune
<i>Silene micropetala</i> Lag.	Caryophyllaceae	—	—	1	—	3	12	Dune
<i>Malcomia ramosissima</i> (Desf.) Thell.	Cruciferae	—	—	—	—	—	2	Dune
<i>Carex arenaria</i> L.	Cyperaceae	—	10	10	—	—	2	Dune
<i>Corema album</i> (L.) D.Don in Sweet	Empetraceae	1	1	3	—	—	—	Dune
<i>Agrostis stolonifera</i> L. var. <i>pseudopungens</i> (Lange) Kerguelen	Poaceae	—	4	5	—	4	3	Dune
<i>Aira praecox</i> L.	Poaceae	—	1	2	4	20	43	Dune
<i>Vulpia alopecuros</i> (Schousboe) Dumort subsp. <i>alopeucos</i>	Poaceae	3	3	9	12	30	33	Dune
<i>Myrica faya</i> Aiton	Myricaceae	1	5	—	—	—	1	Dune
<i>Pinus pinaster</i> Aiton	Pinaceae	4	6	4	—	—	1	Dune
<i>Antirrhinum majus</i> L. subsp. <i>cirrhigerum</i> (Ficalho) Franco	Scrophulariaceae	—	—	3	—	—	—	Dune
<i>Cistus psilosepalus</i> Sweet.	Cistaceae	—	1	1	—	—	—	Dune/generalist ^b
<i>Cistus salvifolius</i> L.	Cistaceae	8	7	24	5	19	7	Dune/generalist ^b
<i>Hypochaeris glabra</i> L.	Asteraceae	—	1	13	—	14	30	Dune/generalist ^b
<i>Pseudognafalium luteum album</i> (L.) Hilliard & B.L.Burt	Asteraceae	—	—	—	—	—	—	Dune/generalist ^b
<i>Senecio vulgaris</i> L.	Asteraceae	3	12	36	3	28	50	Dune/generalist ^b
<i>Anagallis arvensis</i> L.	Primulaceae	—	—	—	—	—	1	Dune/generalist ^b
<i>Cerastium diffusum</i> Pers. subsp. <i>diffusum</i>	Caryophyllaceae	—	—	2	1	1	13	Dune/generalist
<i>Corrigiola litoralis</i> L.	Caryophyllaceae	—	—	—	—	—	2	Dune/generalist
<i>Polycarpon tetraphyllum</i> (L.) L.	Caryophyllaceae	—	—	—	1	6	32	Dune/generalist
<i>Tuberaria guttata</i> (L.) Fourr.	Cistaceae	—	1	5	—	8	11	Dune/generalist
<i>Andryala integrifolia</i> L.	Asteraceae	—	3	26	10	23	45	Dune/generalist
<i>Lactuca virosa</i> L.	Asteraceae	—	2	7	—	5	2	Dune/generalist
<i>Logfia minima</i> (Sm.) Dumort	Asteraceae	—	—	4	—	2	31	Dune/generalist
<i>Senecio lividus</i> L.	Asteraceae	1	2	18	—	1	—	Dune/generalist
<i>Sonchus asper</i> (L.) Hill	Asteraceae	—	—	2	5	—	1	Dune/generalist
<i>Teesdalia nudicaulis</i> (L.) R.Br. In Aiton	Cruciferae	—	—	—	—	5	4	Dune/generalist
<i>Bromus diandrus</i> Roth.	Poaceae	4	—	9	2	22	22	Dune/generalist
<i>Dactylis glomerata</i> L.	Poaceae	3	—	—	—	—	—	Dune/generalist
<i>Vulpia membranaceae</i> (L.) Dumort.	Poaceae	—	—	2	—	—	—	Dune/generalist
<i>Juncus capitatus</i> Weigel.	Juncaceae	—	—	—	—	—	1	Dune/generalist
<i>Cytisus striatus</i> (Hill.) Rothm.	Leguminosae	—	—	—	—	2	5	Dune/generalist
<i>Ulex europaeus</i> L. subsp. <i>europaeus</i>	Leguminosae	15	14	15	4	5	1	Dune/generalist
<i>Fumaria muralis</i> Koch subsp. <i>muralis</i>	Papaveraceae	6	—	1	—	7	3	Dune/generalist
<i>Asterolinum linum-stellatum</i> (L.) Duby in DC	Primulaceae	—	—	—	—	—	8	Dune/generalist
<i>Cerastium glomeratum</i> Thuill.	Caryophyllaceae	—	—	—	—	3	7	Generalist
<i>Silene gallica</i> L.	Caryophyllaceae	—	—	—	—	1	11	Generalist
<i>Anthemis arvensis</i> L. subsp. <i>arvensis</i>	Asteraceae	—	—	—	—	1	9	Generalist
<i>Coleostephus myconis</i> (L.) Reichenb.	Asteraceae	—	—	—	—	—	2	Generalist
<i>Picris echioides</i> L.	Asteraceae	—	1	7	1	—	2	Generalist
<i>Sonchus oleraceus</i> L.	Asteraceae	3	12	21	8	35	36	Generalist
<i>Urospermum picroides</i> (L.) F.W.Schmidt	Asteraceae	—	—	—	9	—	1	Generalist
<i>Cardamine hirsuta</i> L.	Cruciferae	—	4	10	2	7	5	Generalist
<i>Geranium purpureum</i> Vill. In L.	Geraniaceae	1	—	—	5	8	1	Generalist
<i>Briza maxima</i> L.	Poaceae	1	1	16	17	18	11	Generalist
<i>Stachys arvensis</i> (L.) L.	Labiatae	—	—	—	—	—	3	Generalist
<i>Epilobium lanceolatum</i> Sebastiani & Mauri	Onagraceae	—	—	—	—	2	1	Generalist
<i>Polypodium interjectum</i> Shivas	Polypodiaceae	—	4	—	—	—	—	Generalist
<i>Polygonum aviculare</i> L.	Polygonaceae	—	—	2	—	—	1	Generalist
<i>Solanum nigrum</i> L. subsp. <i>nigrum</i>	Solanaceae	—	2	7	—	—	6	Generalist
<i>Centranthus calcitrapae</i> (L.) Dufresne subsp. <i>calcitrapae</i>	Valerianaceae	—	1	—	1	—	1	Generalist
<i>Galium</i> sp.	Rubiaceae	7	4	—	—	—	—	—
<i>Gamochoeta pennsylvanica</i> (Willd.) Cabrera	Asteraceae	—	—	—	—	3	25	Exotic
<i>Coniza bonariensis</i> (L.) Cronq.	Asteraceae	1	11	27	1	29	44	Exotic/invasive
<i>Carpobrotus edulis</i> (L.) N.E.Br.	Aizoaceae	—	—	6	8	3	6	Exotic/invasive
<i>Cortaderia selleana</i> (Schultes) Asch. & Graebner	Poaceae	—	—	—	1	—	—	Exotic/invasive
<i>Acacia longifolia</i> (Andrews) Willd.—only seedlings	Leguminosae	18	30	43	4	14	27	Exotic/invasive
<i>Oxalis pes caprae</i> L.	Oxalidaceae	—	—	—	—	1	1	Exotic/invasive

^a Dune, spontaneous species in sand dune ecosystems, being characteristic to the system; dune/generalist, spontaneous species in several sand ecosystems, including dunes but not exclusively; generalists, species common in disturbed ecosystems, such as ruderals or weeds of cultivated areas; exotic/invasive, exotic species recognized as invasive in Portugal.

^b Species referred as present in the system before the invasion by Sydney golden wattle, even not being characteristic.

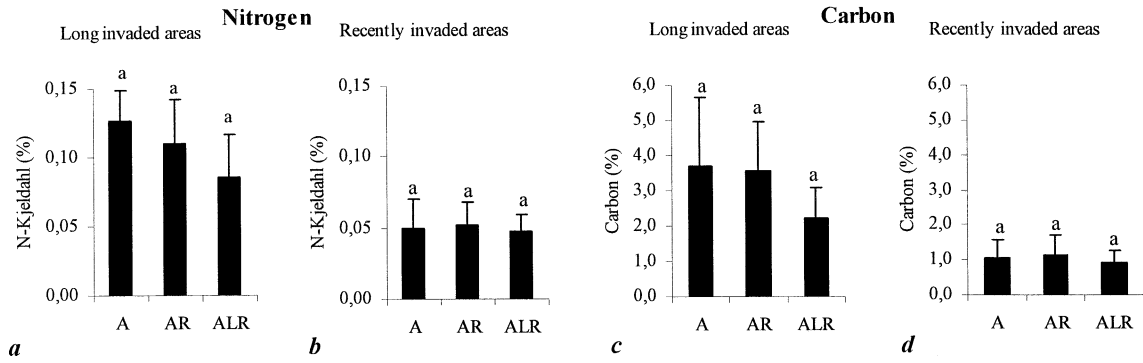


Figure 3. Nitrogen (N—Kjeldahl) (a, b) and carbon (c, d) in soil samples. A, with Sydney golden wattle; AR, Sydney golden wattle removed; ALR, Sydney golden wattle and litter both removed. Bars are average number + SD ($n = 5$). Different letters in bars of same graphic indicate differences statistically significant at $P < 0.05$ (LSD test).

cently cleared of *Acacia* and related this to the change in soil nutrient status. Many of the species were generalists (29.3%) (Table 1), commonly associated with disturbed habitats or weeds, possessing very small, easily dispersed seeds (Raven et al. 1999), and are not characteristic of the system. Dune characteristic species were also observed (19.0% more specific to dune ecosystems, plus 41.3% that emerge spontaneously in habitats associated to sand substrates, including sand dunes) germinating or prevailing from previous established plants, such as the Portuguese crowberry (*Corema album*), fire tree (*Myrica faya*), *Malcomia ramosissima*, or early hair grass (*Aira praecox*). Although rare, seedlings of other invasive species, such as the ice plant and the pampas grass (both 10.3%), also emerged, giving concern about their possible pressure after Sydney golden wattle is removed on a large scale. Ongoing experiments by the authors revealed the same species in the seed banks.

Plots without litter had the highest cover percentage of species recovering (Figures 2c and 2d). The plots where only Sydney golden wattle was removed, particularly on recently invaded areas, showed very similar

results, probably because the thinner layer of Sydney golden wattle litter (see Figure 7a) was not enough to prevent the propagules from appearing.

Soil Recovery. Regardless of time of invasion, all soil parameters analyzed, i.e., total nitrogen (Figures 3a and 3b), carbon (Figures 3c and 3d), pH (Figures 4a and 4b), phosphorus (Figures 4c and 4d), ammonium (Figures 5a and 5b), and nitrate (Figures 5c and 5d), showed similar values in all the three treatments. So far, there is no visible recovery of the system at this level, probably because soil was sampled only 3 mo after treatments were applied. Nevertheless, plots with protracted invasion showed a tendency to a decrease in nitrogen and carbon contents, after litter removal (ALR).

Comparing the two experiments, in the plots where Sydney golden wattle remains (A), nitrogen and carbon contents were higher in long-invaded areas, indicating that the prolonged presence of Sydney golden wattle in the system could be responsible for changes at soil level.

NAG (one of the three chitinases that degrade chitin) activity showed no signs of recovery after the removal

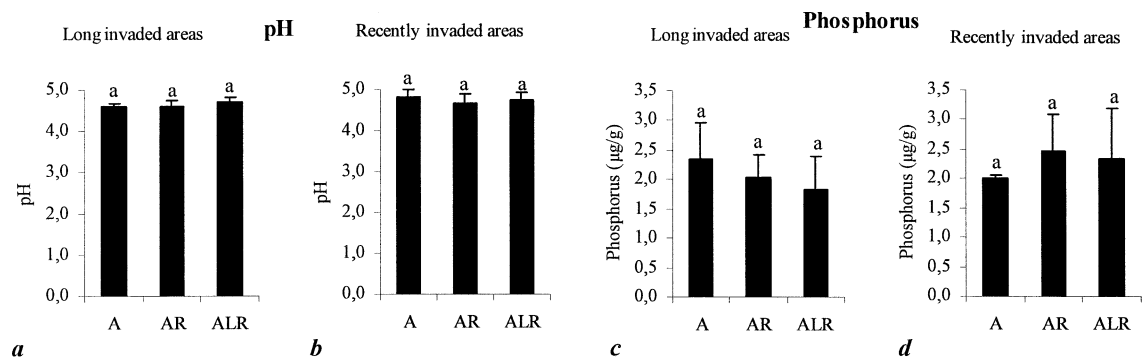


Figure 4. pH (a, b) and phosphorus (c, d) in soil samples. A, with Sydney golden wattle; AR, Sydney golden wattle removed; ALR, Sydney golden wattle and litter both removed. Bars are average number + SD ($n = 5$). Different letters in bars of same graphic indicate differences statistically significant at $P < 0.05$ (LSD test).

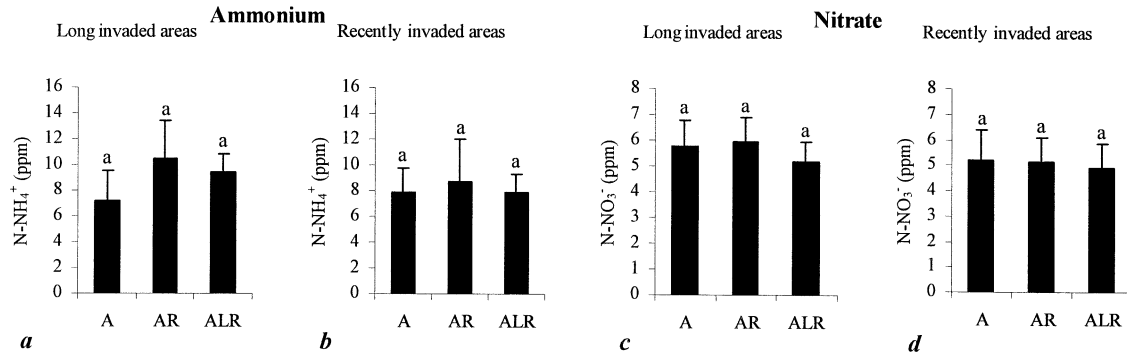


Figure 5. Ammonium (a, b) and nitrate (c, d) in soil samples. A, with Sydney golden wattle; AR, Sydney golden wattle removed; ALR, Sydney golden wattle and litter both removed. Bars are average number + SD ($n = 5$). Different letters in bars of same graphic indicate differences statistically significant at $P < 0.05$ (LSD test).

of Sydney golden wattle (AR) (Figures 6a and 6b). Nevertheless, the prolonged invasion by Sydney golden wattle seems to be promoting an increase of NAG activity in long-invaded areas (compare Figures 6a and 6b). This increase is strongly correlated ($r = 0.82$) with an increase in soil organic matter. Some studies found significant correlations of this enzyme with fungal biomass (Miller et al. 1998) and N mineralization (Ekenler and Tabatabai 2002), suggesting that the presence of Sydney golden wattle is affecting soil community structure and processes.

The litter accumulated in areas invaded by Sydney golden wattle increased with invasion time: long-invaded areas presented a thicker layer of litter when compared with recently invaded areas (Figure 7a). In long-invaded areas, the carbon accumulated in litter was higher (Figure 7b), as it was the percentage of total nitrogen and carbon in the soil (compare treatment A in Figures 3a–d).

Milton (1981) suggested that the change in nutrient status might make the environment less suitable for native plants of fynbos ecosystems invaded by *Acacia* sp. Our results support this suggestion because a higher recovery at floristic level was associated with lower values of carbon, nitrogen, and NAG activity in recently invaded areas. In a recent study, Ehrenfeld et al. (2001) proposed that the enrichment of soil by exotic species may be an important component of the invasive process because alterations to the environment induced by the invasive species may enhance its vigor. Our results suggest that Sydney golden wattle may be facilitating its own invasion by changing the soil characteristics to a state that favors Sydney golden wattle survival at the expense of native species.

These initial results indicate that the invaded systems are still able to recover because a considerable number

of native species are appearing in the plots where control treatments were applied. The response at soil level was not evident at this time. Long-invaded areas seem to suffer a decrease in recovery potential with time as well as accumulating seeds in the soil, which allows rapid re-invasion by Sydney golden wattle after the control methods are applied.

Regarding the control methods, cutting was effective in these trials (even though coppice growth has been recorded in Sydney golden wattle), not only controlling the adult plants but also contributing to deplete the Sydney golden wattle seed bank. Removing litter showed an evident advantage, leading to an improvement in the recovery potential.

Although more monitoring is needed to verify the long-term trends in these trials, an immediate priority should be to clear areas that have recently become invaded by Sydney golden wattle because the restoration effort required after clearance would be less.

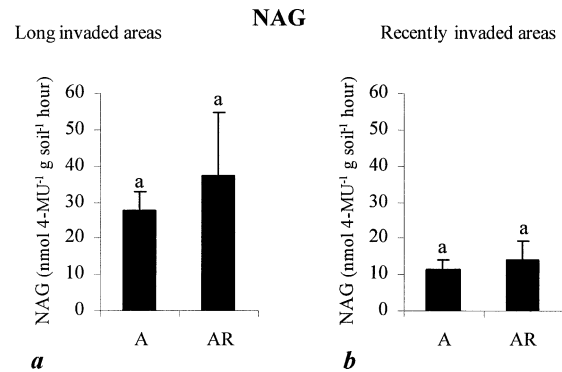


Figure 6. β -Glucosaminidase activity (a, b) in soil samples. A, with Sydney golden wattle; AR, Sydney golden wattle removed. Bars are average number + SD ($n = 5$). Different letters in bars of same graphic indicate differences statistically significant at $P < 0.05$ (LSD test).

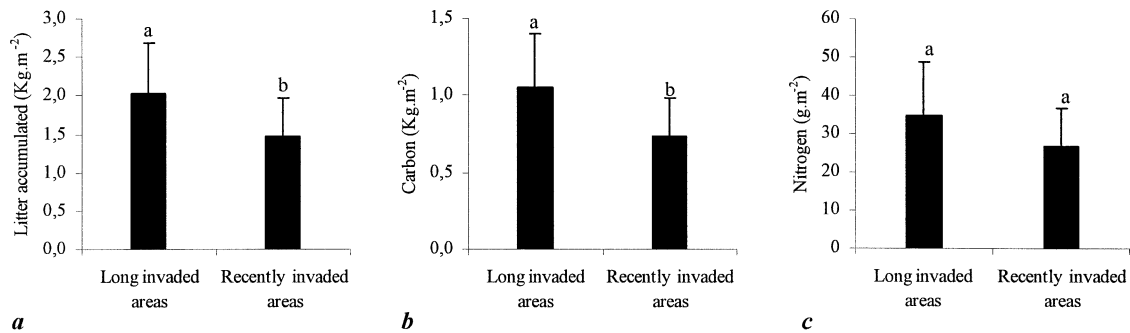


Figure 7. Litter on soil: (a) quantity of litter accumulated; (b) carbon accumulated on litter; and (c) total nitrogen accumulated on litter. Bars are average number + SD ($n = 15$). Different letters in bars of same graphic indicate differences statistically significant at $P < 0.05$ (LSD test).

ACKNOWLEDGMENTS

We thank Francisco Estrompa, Heleno Abreu, Joaquim Santos, and students from Escola Superior Agrária for their valuable help in the mechanical control of golden wattle. Special thanks to John Hoffman for critical comments on the manuscript. This research project—INVADER (POCTI/BSE/42335/2001)—was funded by FCT-MCES, FEDER. E. Marchante was financially supported by a grant from FCT-MCES.

LITERATURE CITED

- Alves, J.M.S., M.D.E. Santo, J. C. Costa, J.H.C. Gonçalves, and M. F. Lousã. 1998. Habitats naturais e seminaturais de Portugal Continental. Lisboa, Portugal: Instituto da Conservação da Natureza. 55 p.
- Baize, D. 2000. Guide des analyses en pédologie. 3^e ed. Institut National de la Recherche Agronomique. eds. Cap. 4. Paris:INRA. Pp. 33–38.
- Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. *J. Veg. Sci.* 7:121–124.
- Bremner, J. M. 1965. Total nitrogen. In C. A. Black, D. D. Evans, J. L. White, L. E. Ensminger, and F. E. Clark, eds. *Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties*. Madison, WI: American Society of Agronomy. Pp. 1149–1176.
- Callaway, R. M. and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521–523.
- Crawley, M. J. 1997. Biodiversity. In M. J. Crawley, ed. *Plant Ecology*. 2nd ed. Cambridge, U.K.: Blackwell Science. Pp. 623–625.
- Cronk, Q. B. and J. L. Fuller. 1995. *Plant Invaders*. London: Chapman and Hall. P. 30.
- Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecol. Appl.* 11:1287–1300.
- Ekenler, M. and M. A. Tabatabai. 2002. β -Glucosaminidase activity of soils: effect of cropping systems and its relationship to nitrogen mineralization. *Biol. Fertil. Soils* 36:367–376.
- Holmes, P. M. and R. M. Cowling. 1997. The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *J. Appl. Ecol.* 34:317–332.
- Kourtev, P. S., J. G. Ehrenfeld, and M. Häggblom. 2002. Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83:3152–3166.
- Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends Ecol. Evol.* 8:133–137.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invisibility. *Ecology* 89:1522–1536.
- Marchante, H. 2001. Invasão dos ecossistemas dunares portugueses por *Acacia*: uma ameaça para a biodiversidade nativa. M.Sc. thesis. University of Coimbra, Coimbra, Portugal. Pp. 65–147.
- Marchante, H., F. Campelo, and H. Freitas. 1999. Ecologia do género *Acacia* nos ecossistemas dunares portugueses. In 1^o Encontro sobre Invasoras Lenhosas. Gerês, Portugal. Pp. 35–41.
- Marchante, H., E. Marchante, and H. Freitas. 2003. Invasion of the Portuguese dune ecosystems by the exotic species *Acacia longifolia* (Andrews) Willd.: Effects at the community level. In L. E. Child, J. H. Brock, G. Brundu, K. Prach, P. Pyšek, P. M. Wade, and M. Williamson, eds. *Plant Invasions: Ecological Threats and Management Solutions*. Leiden, The Netherlands: Backhuys. Pp. 75–85.
- Mc Lean, E. O. 1982. Soil pH and lime requirement. In A. L. Page, R. H. Miller, and D. R. Keeney, eds. *Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties*. 2nd ed. Madison, WI: American Society of Agronomy. Pp. 199–209.
- Miller, M., A. Palojarvi, A. Rangger, M. Reeslev, and A. Kjoller. 1998. The use of fluorogenic substrates to measure fungal presence and activity in soil. *Appl. Environ. Microbiol.* 64:613–617.
- Milton, S. J. 1981. Litterfall of the exotic acacias in the South Western Cape. *J. S. Afr. Bot.* 47:147–155.
- Mooney, H. A. and R. J. Hobbs. 2000. Global change and invasive species: where do we go from here? In H. A. Mooney and R. J. Hobbs, eds. *Invasive Species in a Changing World*. Washington, D.C.: Island. Pp. 425–434.
- Musil, C. F. 1993. Effect of invasive Australian acacias on the regeneration, growth and nutrient chemistry of South African lowland fynbos. *J. Appl. Ecol.* 30:361–372.
- Paiva, J. 1999. *Acacia*. In S. Castroviejo, S. Talavera, C. Aedo, F. J. Salgueiro, and M. Velayos, eds. *Flora Iberica—Plantas Vasculares de la Península Iberica e Islas Baleares. Leguminosae (partim)*, Vol. VII(I). Real Jardín Botánico. Madrid, Spain: CSIC. Pp. 11–25.
- Raven, P. H., R. F. Evert, and S. E. Eichhorn. 1999. *Biology of Plants*. 6th ed. New York: W. H. Freeman.
- Silva, R. 1977. Sector Fertilidade do Solo. Documentação 2. Laboratório Químico-Agrícola. Lisboa: Ministério da Agricultura e Pescas. Pp. 16–21.
- Tavares, M., J. Campos, C. Silva, and F. Caetano. 1999. Estratégias de invasão dos pinhais das dunas do litoral pelas *Acacia dealbata*, *A. melanoxylon* e *A. longifolia*. In 1^o Encontro sobre Invasoras Lenhosas. Gerês, Portugal. Pp. 42–49.
- van Wilgen, B. W., R. M. Cowling, and C. J. Burgers. 1996. Valuation of ecosystems services. *BioScience* 46:184–189.
- Watanabe, F. S. and S. R. Olsen. 1965. Test of an ascorbic acid method for determining phosphorus in water and NaHCO_3 extracts from soil. In A. L. Page, R. H. Miller, and D. R. Keeney, eds. *Methods of Soil Analyses, Part 2: Chemical and Microbiological Properties*. 2nd ed. Madison, WI: American Society of Agronomy. Pp. 413–414.
- Weber, E. 2003. *Invasive Plant Species of the World—A Reference Guide to Environmental Weeds*. Oxford, U.K.: CABI Publishing. 548 p.
- Whibley, D.J.E. 1980. *Acacias of South Australia*. South Australia, Australia: D. J. Woolman. Pp. 6–10.